Proximate and ultimate determinants of reproductive skew in the polygyne ant *Formica fusca*

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The thesis is based on following articles or manuscripts, which are referred to in the text by their Roman numerals:

I Hannonen, M., Helanterä H., Sundström, L.: Habitat age, breeding system and kinship in the ant *Formica fusca.* – Manuscript.

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The following table shows the major contributions of authors to the original articles or manuscripts.

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Summary

Introduction

In many vertebrate and invertebrate taxa members of a society come to share reproduction, and cooperatively rear offspring (eg. Krebs & Davies 1997). This often occurs at the expense of the personal reproduction of some individuals in the group, to the benefit to other group members. Such reproductive division of labour can eventually become manifest as differential reproductive potential among members of the society. For example, in most vertebrate societies and some invertebrate societies all group members have the potential to reproduce. However, in many invertebrate societies, most notably among social Hymenoptera (ants, bees and wasps), only one individual, the colony queen, has retained the full reproductive capacity and colony workers do not reproduce at all.

Kin selection theory provides a framework for analysing the rules by which such reproductive division of labour can evolve (Hamilton 1964a,b). The theory holds that a reduced personal reproduction can be outweighed by the benefits gained through helping relatives increase their reproductive output, thereby also passing on genes shared with the altruist (Hamilton 1964a,b). In social insect colonies where only one, single-mated queen reproduces, colony members are highly related to each other and kin selection can be seen as an explanation for the evolution and maintenance of reproductive altruism. However, the kin structure often varies among colonies either owing to variation in queen number or owing to variation in queen mating frequency (Hölldobler & Wilson 1977; Buschinger 1974; Page 1986; Fletcher & Ross 1985; Ratnieks & Boomsma 1995). The presence of multiple related queens and/or multiple patrilines dilutes the relatedness among colony members, and thus the fitness returns from helping. However, as an extra bonus intracolony conflicts due to high relatedness asymmetries also decrease (Bourke & Franks 1995). Nevertheless, the presence of several matri- and patrilines within one colony will create new conflicts with respect to brood composition and reproductive apportionment among both queens and workers. Hence, social life is far from a harmonic coexistence where members of the society behave unselfishly (Bourke & Franks1995; Crozier & Pamilo 1996; Keller & Reeve 1999)

In ants the principal cause of variation in social structure, both between and within species, is the variation in queen number (Bourke & Franks 1995). There are several types of polygynous colonies, of which the key distinction can be made between primary and secondary polygyny (Hölldobler & Wilson 1977). Primary polygyny occurs when several queens found a new colony together (foundress association). However, such foundress associations usually retain only one queen, because after the first workers have emerged, the queens fight until only one queen is left, or alternatively, the workers eliminate all but one one queen (Hölldobler & Wilson 1990; Heinze 1993; Bourke

& Franks 1995). Secondary polygyny occurs when mature colonies, founded by a single queen, recruit offspring females back to their natal colony. This kind of permanent coexistence of several queens is common in ants, as about half of the European ant species are known to be polygynous (Buschinger 1974). Such polygyny can be considered as a second round of social evolution (Rosengren & Pamilo 1983), as these queens are by definition co-breeders and contribute collectively to the worker force of the colony, but also compete for reproductive shares within a colony of limited resources.

When several queens come to share reproduction within a colony, there will be more than one matriline and patriline among the brood. Workers, therefore, will raise offspring to which they are less closely related than full sibs and their kin-selected benefits gained from altruistic behaviour decreases. In addition, queens have to share the limited resources of their colony, which is further reflected by the fact that an increase in queen number is generally associated with a decrease in individual reproductive output (Keller & Vargo 1993; Bourke & Franks 1995, but see Walin et al. 2001). Moreover, several recent studies have shown that queens in multi-queen societies do not contribute equally to the offspring produced by the colony (Reviewed by Reeve et al. 1998; Reeve & Keller 2001). Consequently, the coexistence of several queens raises an interesting evolutionary problem: why do young queens join resident queens in established colonies, and why do workers and resident queens accept them (Keller 1995; Bourke & Franks 1995). Kin selection, defined by the joint effects of relatedness between interacting individuals and environmental factors (Hamilton 1964a, b) predicts the evolution of polygyny under three conditions; First, when dispersal risks are high or colony founding success low for young queens attempting to establish colonies independently (Rosengren & Pamilo 1983; Herbers 1993; Rosengren et al. 1993; Nonacs. 1993). Second, if the probability that a colony loses its queen is high (Nonacs 1988; Pamilo 1991), and third, if queen life span is short compared to the potential life span of a colony (Nonacs 1988; Pamilo 1991).

After new queen has joined and she has been accepted into the colony, co-breeding queens may come into conflict over reproductive shares, as each queen is expected to maximize her individual reproduction at the expense of the reproduction of her competitors. Reproductive skew theory builds on the foundation provided by inclusive fitness principles and seeks to generate predictions concerning the partitioning of reproduction in societies with multiple reproductive individuals (Reeve & Ratnieks 1993; Keller & Reeve 1994; Cant 1998; Reeve et al. 1998; Cant & Johnstone 1999; Johnstone & Cant 1999a, b; Johnstone et al. 1999; Kokko & Johnstone 1999; Johnstone 2000; Reeve 2000; Reeve & Emlen 2001; Reeve & Keller 2001). The term reproductive skew describes how reproduction is shared among co-breeding individuals, such that high skew stands for uneven reproduction, and low skew stands for equal reproduction. The numerous reproductive skew models can be divided into two main groups based on the assumptions on the nature of dominance among group members (Johnstone 2000; Reeve & Keller 2001). The "transactional models" assume that either the dominant (concession models, eg. Reeve & Ratnieks 1993) or the subordinate (restraint model, Johnstone & Cant 1999a) has total control over reproductive sharing in the group. In contrast "tug-of-war models" (Reeve et al. 1998), assume that dominants and subordinates both have limited control over the reproductive

Table 1. Predictions of the basic models described in text. The effect of each parameter assumes that other parameters and group size are held constant (adapted from Reeve and Keller, 2001)

	Transactional models		Tug-of-war- model[3]
Variable	Concession model[1]	Restraint model[2]	
Group output increases relative to the potential output of a solitary individual	Reproductive skew increases	Reproductive skew decreases	No change in reproductive skew
Relatedness between co-breeders increases	Reproductive skew increases	Reproductive skew decreases	No change or skew decreases
Aggression between co-breeders increases	Reproductive skew increases	decreases	Reproductive skew

1. Reeve and Ratnieks, 1993; Reeve and Keller, 2001
2. Johnstone and Cant, 1999
3. Reeve et al., 1998.

allocation, and thus both face a trade off between maximising overall group productivity versus their own share of reproduction. The models yield specific sets of predictions concerning the effects that factors such as ecological constraints, relatedness, fighting ability and group productivity are expected to have on the degree of reproductive skew (Table 1).

However, as Johnstone (2000) pointed out, the relevant model to be tested cannot be selected unless the assumptions on which the predictions of the models are based have been confirmed for the study species. Both "transactional" and "tug-of-war" models were developed for societies where co-breeders have the option to reproduce independently and where the decision upon reproductive shares is made among the individuals directly involved in reproduction. These scenarios may not necessarily apply in polygyne ant societies. First, queens have lost their wings and so do not have the option to leave the colony and begin independent breeding, unless colonies can reproduce by budding. Second, the workers may act as an independent party with their own reproductive interests. Indeed, workers are in a position to influence both the reproductive shares of queens, as well as the number of reproductively active queens (Keller & Vargo 1993; see also Bourke & Ratnieks,1999). Recent extensions to the traditional reproductive skew models incorporate the effect of workers, defined as the "collective" dominant, as distinct from the queens one of which may become the "virtual" dominant, (Reeve & Keller 2001). Hence the workers are the party in control and exert their reproductive interests by favouring the queen they are more closely related to ("virtual dominant").

The aim of this study is to investigate both ultimate and proximate factors determining reproductive sharing in multiple queen colonies of the ant *Formica fusca* by using the framework provided by kin selection theory. The reproductive skew models provided parameters to test outcomes of the potential

conflict among queens and between workers and queens over individual queen's reproductive shares (**I, II, V**). However, when studying evolutionary outcomes of within-colony conflicts, it has to be kept in mind that there are several levels at which selection may act: the genes, which are ultimately transmitted over generations, are packed in individuals, individuals in colonies, and colonies in populations (Keller & Reeve 1999). As ultimate factors we analysed ecological constraints acting at population level (**I**), and relatedness, size difference and total production among co-breeders all acting at colony level (**II, V**). As proximate factors we analysed behaviour and chemical communication among and between society members (**III, IV, V**).

Sophisticated molecular and chemical techniques, such as analysis of microsatellites and cuticular hydrocarbons, have played an important role in this study to elucidate determinants of skew among co-breeding queens both at proximate and ultimate levels (**I–V**). By analysing determinants of reproductive skew new insights can be gained regarding factors that affect the partitioning of reproduction, not only in polygyne ant colonies, but also in co-breeding animals in general (Keller & Reeve 1994; Reeve & Keller 1995; Sherman et al. 1995).

Ultimate determinants of reproductive skew

In ants, founding a new colony alone involves dispersal from the nest for the mating flight, followed by colony foundation alone. Hence, factors that decrease survival during dispersal or solitary colony founding, such as habitat saturation (nest-site limitation) and patchiness, will act as constraints on dispersal and promote polygyny (e.g. Rosengren & Pamilo 1983; Hölldobler & Wilson, 1977, 1990; Herbers 1986; Rosengren et al. 1993; Seppä et al. 1995; Bourke & Heinze 1994). In *Formica fusca* both the mating system and colony kin structure vary between populations in habitats with different ecological constraints (**I**). The significant inbreeding found among workers in the population living in saturated and patchy habitat suggests that dispersal is considerably restricted, both for males and for females. In contrast, no inbreeding was found within the population inhabiting habitat where dispersal was not restricted with ecological constraints (**I**).

The average degree of reproductive skew within polygynous societies is influenced by similar ecological factors as polygyny. When ecological constraints limit dispersal and make solitary colony founding costly, the daughter queens should seek adoption to their natal colony and hence tolerate lower personal reproduction because the chances to reproduce alone are small. Therefore, at the population level, habitats with high costs for solitary breeding should promote high reproductive skew among co-breeding queens compared to habitats with low costs for solitary breeding (Vehrencamp 1983a, b; Reeve & Ratnieks, 1993; Keller & Reeve, 1994). An association between high skew and strong ecological constraints has been found in polygyne leptothoracine ants (Bourke & Heinze 1994) and also suggested in polygynous *Formica fusca* (**I**). Given that high costs of dispersal increase the propensity of daughter queens to seek adoption within natal colony, ecological constraints should also be reflected by increase in relatedness among co-

breeding queens. Increased skew can further increase relatedness among queens, when these are adopted into their natal colony, because increased skew decreases the effective number of breeders (Heinze 1995). Indeed, in a comparison between populations, a positive association between queen–queen relatedness, ecological constraints and reproductive skew has been found among leptothoracine ants (Bourke & Heinze 1994). The queen–queen relatedness was also slightly higher among *F.fusca* queens in the saturated habitat with fewer suitable nest sites compared to relatedness among queens in the habitat with continuous habitat (**I**).

At the colony-level relatedness among co-breeders is predicted to determine skew in all skew models (Johnstone 2000). However, the prediction of an association between relatedness and reproductive skew within breeding associations depend both on assumptions and other parameters incuded in the model (*Positive association* eg. Vehrencamp 1983a,b; Reeve & Ratnieks 1993; Reeve & Keller 1995. *Negative association* Reeve et al. 1998; Johnstone & Cant 1999a. *No association at all* Reeve 1998; Reeve et al. 1998). To date few studies have investigated within-colony variation in relatedness and reproductive skew among queens in polygynous ants. In *Myrmica tahoensis* reproductive skew was independent of queen–queen relatedness (Evans 1996). In the ant *Leptothorax rugatulus* the average skew was also independent of queen–queen relatedness (Rüppel et al. 2002). However, in the production of sexual offspring, the skew in *L.rugatulus* queen associations was significantly negatively correlated with queen–queen relatedness. Similarly, in *F. fusca* the relatedness among queens was significantly negatively correlated with reproductive skew: the higher the relatedness among queens, the more equally they shared their reproduction (**II**). At the colony level the relatedness among nest mate queens is the most important determinant of the degree of reproductive skew in *F. fusca* (**II**). By contrast, other factors such as fighting ability as reflected by size differences within queen association, or the productivity of the group had no effects on the degree of skew (**II**). In addition, the fact that the effective number of queens, expressed through worker relatedness, is not associated with skew suggests that the genetic affinity between queens, rather than the general kin structure of the colony dictates skew in *F.fusca* (**I, II**).

Also the workers in a colony are in a position to regulate the reproductive output of individual queens because they rear the brood (Keller & Vargo 1993) and hence may exert their reproductive interests by favouring the queen they are more closely related to. A recent extension of reproductive skew models incorporates workers as potential actors in determining the reproductive shares of queens (Reeve & Keller 2001). This model takes into account the strength of the incentive for workers to manipulate brood composition, and predicts that when workers are more related to one queen than to the others, the workers should exert their reproductive interests by selectively rearing the offspring of the queen of closest kin. Conversely, when workers are equally related to all queens, they have no incentive to selectively rear offspring of one particular queen. The "workers as a collective dominant" scenario (Reeve & Keller 2001) might actually explain the negative correlation between skew and relatedness among queens (**II**). If co-breeding queens are full sisters most workers will be more equally related to both queens and will have no kin-selected incentive to favour one queen over the other, which would result in low

skew. In contrast, when queens are unrelated or of low relatedness, most workers may be more related to one of the queens. If workers favour the queen of closest kin, high skew would ensue. As a result a negative association between relatedness and reproductive skew would arise. However, in queen associations of *F.fusca* the queen more closely related to the workers did not attain a higher reproductive share compared to the more distantly related queen (**V**). Instead, the fecundity of a queen was the main determinant of her absolute reproductive apportionment (**III–V**). Hence, the relatedness of workers to individual queens does not directly determine the reproductive skew among queens.

The "workers as a collective dominant" – scenario is akin to the concept of nepotism, which holds that closer kin should be favoured over more distant relatives (Shermann et al. 1997). Several studies have tried to demonstrate nepotism, but to date the evidence has been either inconclusive or negative (Reviewed in Keller, 1997; Keller & Reeve 1999). The lack of nepotism within insect societies has been explained with three hypotheses (Reviewed in Keller 1997; Keller & Reeve 1999). The first one suggests that differential treatment of colony members would lead to losses in colony efficiency, because time is wasted for assessment of genetic relatedness (Ratnieks & Reeve 1992). The second explanation proposes that nepotism is disfavoured because the high frequency of recognition errors dilute the benefit of nepotism so that the benefit no longer exceeds the cost (Shermann et al. 1997). Finally, the third explanation posts that some colony members will benefit from scrambling the recognition labels or by reducing or eliminating information about kinship within the group (Reeve 1998).

Even though the relatedness between workers and individual queens did not explain the final reproductive shares among queens in *F.fusc*a (**V**), we found that the brood composition changed as a function of the relative kin value of queens. The higher the relative kin value of a queen, the more her representation among the offspring increased during brood rearing (**V**). Our result suggests that workers of *F.fusca* can recognise kin and enhance their inclusive fitness by selfishly manipulating brood composition (**V**). This is the first study to show nepotism, manifest as favouring of the offspring of closer kin among brood of several co-breeding queens. Hence, beside the relatedness among colony queens, also the relatedness between workers and queens had slight effect on the skew as the relatedness significantly affected the changes occurring in brood compositions during brood rearing (**V**).

Proximate determinants of reproductive skew

Proximately, queens that share the same colony may solve the reproductive conflict either by aggressive behaviour and/or by pheromonal signalling (Fletcher & Ross 1985; Keller & Nonacs 1993). In many social insect species queen fecundity reflects social rank formed by aggressive acts (e.g. Heinze & Smith 1990; Oliveira & Hölldobler 1990; Visscher & Dukas 1995; Ortius & Heinze 1999). Another means for queens to manipulate reproductive skew through physical actions is selective egg cannibalism, but this has never been shown to occur among social insects (Bourke 1991, 1993, 1994). In *F.fusca*,

the queens do not behave aggressively towards each other, and they do not affect skew by cannibalising eggs, so aggressive behaviour apparently does not greatly affect reproductive skew among queens (**IV**). Also in other eusocial species aggressive behaviour within permanent queen-associations is rare or absent (Heinze 1993; Keller & Vargo 1993). This may be the result of the size of the colony; the energy invested to control reproduction by aggressive acts increases with the colony size. Instead by using chemical signals queens may profit from avoiding investment of time and energy in repeated conflicts (Ayasse et al. 1995). This may have led to the evolution of efficient pheromonal queen signals in highly eusocial species with large colony size (Reeve & Ratnieks 1993).

There are two possible mechanisms, which may account for the pheromonal signalling: the pheromone may act directly on the physiology of the co-breeding queen; or workers may use the pheromone as a signal to regulate queen reproductive output (Keller & Nonacs 1993). The first mechanism is likely to be evolutionarily unstable, as the queen inhibiting egg production of the competitor might harm herself as well (Keller & Nonacs 1993). By contrast, a signal indicating the presence of a queen and her fecundity, is evolutionarily stable, as the receivers (in this case workers) increase their inclusive fitness by responding to it (Keller & Nonacs 1993). Such queen signals are also expected to be honest because workers only benefit if they judge queen productivity correctly (Keller & Nonacs 1993). Queen fecundity attracts workers (Keller 1988; Keller & Passera 1989; Sommer & Hölldobler 1995; Ortius & Heinze 1999) suggesting that the onset of oogenesis causes a modification of some external characteristics of queens on which recognition is based. Indeed, there are several experimental studies indicating that workers are able to assess queen fecundity (Fletcher & Blum 1983; Keller & Ross 1998; Peeters et al. 1999; Ortius & Heinze 1999; Liebig et al. 1999; Gobin et al. 1999; **III**) as well as discriminate between co-breeding queens (Sommer & Hölldobler, 1995; Ortius & Heinze 1999; **III**).

The insect cuticle is covered with a layer of waxes of which the main constituents are non-volatile hydrocarbons, whose primary function is to provide protection from desiccation (Lockey 1988). Because of the large variability in their chemistry, cuticular hydrocarbons (CHC) are used in variety of contexts among social insects, such as species recognition (reviewed by Singer 1998), nestmate recognition (Espelie et al. 1994; Lahav et al. 1999) and advertisement of social status (Peeters et al. 1999). Several studies have reported a correlation between ovarian activity and a specific blend of cuticular hydrocarbons in social insects, for instance in the queenless ants *Dinoponera quadriceps* (Monnin et al. 1998; Peeters et al. 1999), *Harpegnathos saltator* (Liebig et al. 2000) and *Diacamma ceylonense* (Cuvillier-Hot et al. 2001), the wasp *Polistes dominulus* (Sledge et al. 2001), and the ant *F. fusca* (**III**). What the study of *F.fusca* adds to the previous results on the workers ability to recognize queen fecundity (Fletcher & Blum 1983; Keller & Ross 1998; Peeters et al. 1999; Ortius & Heinze 1999; Liebig et al. 1999; Gobin et al. 1999) and the connection between queen cuticular chemistry and ovarian activity (Monnin et al. 1998; Peeters et al. 1999; Liebig et al. 2000; Cuvillier-Hot et al. 2001; Sledge et al. 2001) is that the results of *F.fusca* indirectly suggest the existence of a link between reproductive activity, CHC profile and worker attention among queen associations consisting of fertile and breeding queens (**III**).

The results of two independent studies of *F.fusca* suggest that queen fecundity at the onset of brood rearing is a good indicator of her final reproductive output, although changes in brood composition may occur during brood development (**III–V**). Differences in queen fecundity may arise if phenotypic traits or age correlate with the intrinsic fecundity of queens (Keller 1993; Keller & Ross 1993). Differences in fecundity have been demonstrated in a large number of organisms and there is generally a strong genetic component, which affects phenotypic differences. If fecundity differences are genetic, the explanation predicts that skew should be lower in colonies in which queens are genetically more similar because they are highly related. This interpretation is consistent with the negative correlation between relatedness and reproductive skew that was found (**II**).

It is also possible that differences in fecundity, as seen only in the reproductive differences of each independent study year (**II–V**), are associated with differences in queen age (Brian 1988; Bourke 1991; Keller 1993). A high rate of queen turnover, which has been demonstrated in several species of polygynous ants (Seppä 1994; Evans 1996; Bourke et al. 1997; see also Heinze & Keller 2000), leads to the co-existence of queens from different age cohorts within a same colony. Given a high rate of queen turnover, queens of the same age may have the same mother and thus may be more closely related compared to queens from different age cohorts, which may be more likely to have different mothers. If queen fecundity reflects her age**,** then queen associations comprising queens of similar age will have similar fecundity, and consequently will share reproduction more equally (low reproductive skew), than in associations where queens belong to different age cohorts. Thus, age-specific fecundity may also lead to a negative association between relatedness and reproductive skew among queens, as shown in *F.fusca* (**II**).

Alongside indirectly manipulating the skew through unequal attention to queens according to their egg-laying activity (**III**), workers may directly regulate the reproductive output of individual queens during brood rearing (Keller & Vargo 1993; **IV–V**). Indeed, workers are in good position to do this as they take care of the brood during the time the eggs laid by the queens develop to adults. To date several studies have shown that workers selectively affect brood sex ratios according to their kin-selected optima (Sundström 1994; Sundström et al. 1996; Foster & Ratnieks 2000; Hammond et al. 2002; Chapuisat & Keller 1999; Queller & Strassmann 1998; Sundström & Boomsma 2001). However, no previous studies had investigated whether workers manipulate the reproductive shares of co-breeding queens. Workers may selectively rear brood of favourite queens and/or eliminate the brood of less favoured queens. This should result in changes in reproductive apportionment of queens during brood development from eggs to pupae. In *F.fusca* we observed changes in brood compositions between egg and pupal stages, which were associated with the relatedness between queen and workers (see above; **V**). However, the association was only found when the strong effect of queen egg laying activity on her final reproductive share was eliminated. Therefore, our study adds an extra hypothesis for the lack of evidence in support of nepotism: We suggest that the evidence for kin recognition in workers may be weak or missing partly due to difficulties in detecting preferential treatment because a multitude of factors may affect the final brood composition. In *F.fusca* the difficulty in detecting nepotism was hidden under strong

factor of queen fecundity, which seems to be the key proximate determinant of queens' reproductive partitioning within multi-queen associations of *F.fusca* (**II–V**).

Conclusions

This study shows how the interplay between ultimate and proximate factors affects reproductive skew among co-breeding queens of the ant *Formica fusca*. At the population level, the genetic relatedness among nestmate queens was slightly higher in patchily distributed old habitat with few potential nest sites compared to that among queens in the new habitat with better opportunities for dispersing and solitary colony founding (**I**). This is consistent with the prediction that higher costs for independent colony founding lead to an increased tendency of daughter queens to seek adoption within their natal colony despite a decrease in their personal reproduction. However, the reduced personal reproduction can be outweighed by the inclusive fitness benefits gained through reproduction of a close relative in the natal colony. In addition, such adopted queens may inherit the reproductively dominant position later (Ragsdale 1999; Kokko & Johnstone 1999). Also, as pointed out by Heinze (1995), in habitats with ecological constraints on dispersal it may be difficult to discriminate between causes and consequences between high relatedness and high skew, as high skew leads to high relatedness among the very same offspring, which eventually may be adopted to the colony (**I**).

At the colony level, queen fecundity, measured as queen egg laying rate, is the most important proximate determinant for the final reproductive output of a queen (**III, IV**). Workers of *F.fusca* seem to be able to discriminate among co-breeding queens according to their fecundity, probably through a fecundity signal encoded in the cuticular hydrocarbon profile of the queen (**III**). Workers respond by allocating care towards queens as a function of the strength of the signal. Workers may have evolved to recognize and act upon the fecundity signal at the beginning of the reproductive season to enhance the productivity and longevity of the colony, which is presumably advantageous both for workers and queens.

Queen fecundity may be determined either solely by queen phenotype or by queen age but most probably by a combination of both (Brian 1988; Bourke 1991; Keller 1993; Keller & Ross 1993). The variation in queen relatedness may also reflect variation either in queen phenotype and/or age (**II**). The queens of similar phenotypes or of same age group are likely to share common genes and are hence more closely related than queens of different phenotypes or of different age groups. Hence, the correlation between relatedness and reproductive skew within queen associations of *F.fusca* can be explained by differences in fecundity either through differences in queen phenotype and/or age (**II**). In addition, worker attention may also work as a reinforcement for the level of fecundity of an individual queen because food supply has been shown to influence queen fecundity (Tschinkel 1988; Brian 1989; **III**).

This study highlights the interplay between ultimate and proximate factors as determinants of reproductive partitioning in multi-queen colonies of the ant

F. fusca. In addition, it demonstrates how power affiliations may be complex within colonies where different parties, in this case individual queens and workers, pursue their individual genetic interests. Workers of the ant *F.fusca* can recognize kin and selectively raise brood laid by the queen of closer kin (**V**). By selective offspring rearing workers attempt to increase the proportion of brood produced by queens closer kin to them and so increase their kin selected benefits (**V**). However, these selfish efforts, even though significant, do not exceed the dominance of queen fecundity in determining her reproductive share (**III, IV**).

The results of this study form a direct link from proximate to ultimate determinants of reproductive skew within insect societies and highlight the importance of analysing reproductive sharing across the entire life spans of individuals when trying to understand the connected multiple mechanisms which determine the reproductive skew within breeding societies. In the future, the effect of queen age and phenotype on the fecundity and on reproductive skew within polygyne colonies will deserve exploration.

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